

The concept of correlated progression as the basis of a model for the evolutionary origin of major new taxa

T. S. Kemp^{1,2,*}

¹*Oxford University Museum of Natural History, Parks Road, Oxford OX1 3PW, UK*

²*St John's College, Oxford OX1 3JP, UK*

Understanding the evolutionary processes responsible for the long treks through morphospace associated with the origin of new higher taxa is hampered by the lack of a realistic and usable model that accounts for long-term phenotypic evolvability. The systems-related concept of correlated progression, in which all the traits are functionally linked and so constrained to evolve by small increments at a time in parallel with each other, provides the basis for such a model. Implications for the process of evolution at high taxonomic level are that: the evolving traits must be considered together as a system, and the exact sequence of incremental changes in characters is indeterminable; there are no identifiable key innovations; selection acts on the phenotype as a whole rather than on individual traits; and the selection force is therefore multidimensional. Application of the model to the pattern of evolution of traits and trait states as revealed by the fossil record of the stem groups of such taxa as mammals, turtles and tetrapods generates realistic testable hypotheses about how such groups evolved.

Keywords: correlated progression; evolvability; macroevolution; higher taxa; origin of tetrapods.

1. INTRODUCTION

For all its fundamental biological interest, the study of evolutionary processes leading to major transitions—the origin of basic body plans and new higher taxa—is remarkably neglected in the evolutionary literature. To a large degree, this is because it is overshadowed by the experimental, mathematical and computer tractability of far simpler systems, like the behaviour of a small number of alleles or traits in a simple adaptive landscape with a single selective focus. The prevailing assumption is that higher taxa arise by no more than such microevolutionary processes acting for long enough; therefore, all that is required to explain the origin of some particular new higher taxon is the conceptually trivial description of the contingent environmental circumstances, and therefore selective forces, to which the evolving lineage was exposed. However, interpretations of actual cases of evolutionary transitions associated with large changes in many characters, notably those inferred from the fossil record, are profoundly unsatisfactory when constrained by such simple models, even though there is little agreement on what might constitute a more realistic conceptual basis.

Central to any theoretical consideration of evolution at this level is the idea of evolvability. Major evolutionary transitions, by definition, involve long treks through morphospace by a sequence of phenotypes, during the course of which a large number of traits change, often to a considerable extent. There is an apparent conflict between evolvability, the property of an organism to evolve by serial accumulation of mutations affecting a single trait at a time, and phenotypic integration, in which the phenotypic traits interact functionally with one another in precisely

determined ways. Integration of the many traits potentially inhibits evolutionary change in any one of them without a loss of overall phenotypic fitness.

(a) *Modularity*

A large literature has grown up in recent years, developing and debating the view that resolution of the evolvability paradox lies in the modular structure of organisms and their developmental mechanisms (e.g. Wagner & Altenberg 1996; Kirschner & Gerhart 1998; Schlosser 2002, 2004; Eble 2004a,b; Griswold 2006). Others (Dassow & Munro 1999; Nagy & Williams 2001; Kemp 2007) have argued that modularity, the proposed existence of ‘semi-independent’ units, while undoubtedly a useful device for describing organisms, and also a valuable model for understanding the architecture of the developmental system, cannot account for the existence of the property of phenotypic evolvability. Firstly, there is too extensive a degree of interaction between all the different parts and processes of the organism, many of which such as locomotory, nervous and circulatory systems lack the properties of modules. Secondly, there is an absence of any consistent correspondence between recognized developmental and descriptive phenotypic modules. Each part of the phenotype is affected by a range of developmental modules; each developmental module affects a range of phenotypic parts.

(b) *Correlated progression*

An alternative resolution of the phenotypic evolvability problem is logically related to systems analysis, in which the nature of the functional and structural interrelationships of the parts are considered more important, while the parts or characters themselves are regarded as somewhat arbitrary abstracts of the whole. The history of this mode of thinking

*tom.kemp@oum.ox.ac.uk

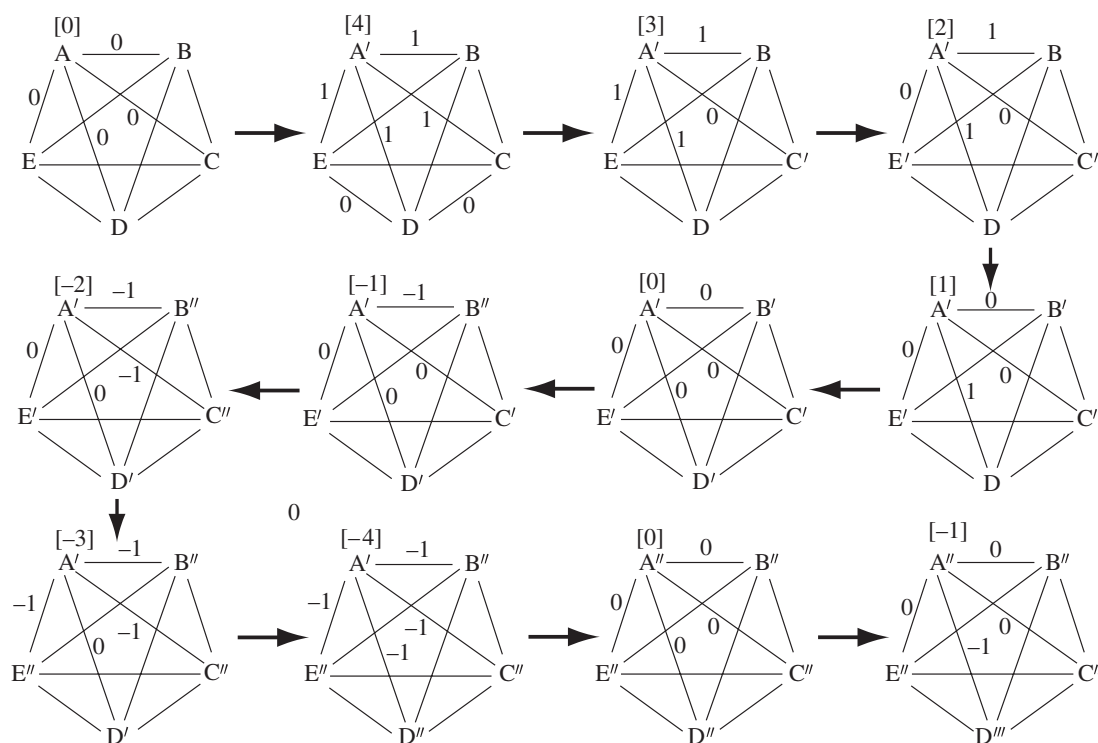


Figure 1. Correlated progression model. A succession of evolutionary steps involving five phenotypic traits (A–E). The traits are mutually interconnected by slightly flexible functional linkages, represented by the lines. Any trait may evolve but only by a single increment at a time, for example A to A' or B' to B''. Any trait may be one increment ahead of any other (+1), at the same level as another (0), or one increment behind another (–1). A measure of how potentially evolvable is a particular trait at a particular instant is indicated by the sum of its linkage values: the lower the figure, the less constrained and therefore the more probable that a further incremental change will occur. The manner in which this value for one trait varies over time as other traits evolve is illustrated for trait A, where the value varies from –4 to +4 at different stages in the evolutionary progression.

can be traced back to Aristotle (Konopka 2007), and its implications for character analysis and evolvability have been discussed in more recent years by several authors (e.g. Dullemeijer 1974; Wagner & Laubichler 2000; Schwenk 2001). Contemporary versions of systems theory are used by functional biologists in the context of complex structures and their control (Ceste & Doyle 2002), and by molecular biologists studying integrated networks of biomolecules in the cell (Palsson 2006; Alon 2007). The descriptive concept for long-term phenotypic evolvability that emerges from this approach is termed correlated progression (Thomson 1966; Kemp 1985, 1999; Lee 1996; Budd 1998).

2. THE CORRELATED PROGRESSION MODEL

The correlated progression model of evolution (figure 1) is predicated on the commonplace expectation that, in principle, all the structures and processes, referred to here as the traits of an organism, are integrated in such a way that ultimately each one is both dependent on and necessary for the functioning of all the others in a well-adapted phenotype. (The difficult question of what exactly constitutes a 'character' is not addressed here; for extensive discussions see the volume edited by Wagner (2001).) Any one trait is described as functionally linked to all of the others, either directly or indirectly via intervening traits. The model makes a number of further assumptions about the nature of the functional linkages and traits, which are as follows:

- (i) The functional linkages between any particular trait and other traits are sufficiently flexible that a

small, though only a small, incremental change may be possible in that trait at any instant in evolutionary time without losing its integration in the organism as a whole.

- (ii) The functional linkages between the various traits differ in how flexible they are, or in Budd's (2006) terminology, how constrained by one another the traits are. At any instant in evolutionary time, some traits are freer to undergo incremental change than others without losing their functional integration in the organism as a whole. This will be a transient state of affairs for any one such trait, because the degree of flexibility of its functional linkages will change with incremental changes in the traits to which it is connected (figure 1). Conversely, at any instant, several to many traits will be connected by sufficiently flexible functional linkages for any one of them to evolve by an increment.
- (iii) Genetic variation occurs in most of the traits for most of evolutionary time. It is universally appreciated that artificial selection can affect almost any trait of an organism that is chosen, indicating the presence of existing genetic variation in virtually all of them (Lewontin 1974; West-Eberhard 2003).
- (iv) Natural selection acts on the fitness of the organism as a whole, and not exclusively on any single trait. Modelling a simple system with an assumed selective force for a single or perhaps a pair of phenotypic traits is a common analytical technique for both simulated and real cases, but tends to ignore the otherwise uncontroversial view that, in so far as

fitness relates to reproductive probabilities, everything an organism is and does contributes to it. Even if directional selection appears to be acting on one focal trait, at the very least stabilizing selection is acting on all the others.

It is a corollary of these assumptions that the pattern of evolution of new traits and trait states along a lineage that spans the morphological distance from ancestral state to a new higher taxon will be thus:

- (i) The pattern of acquisition of new traits or trait states from the ancestral to the descendant phenotype consists of small changes in one trait at a time, spread over the whole set of traits. They evolve analogously to a line of people walking forwards hand in hand: any one of them can be a single pace in front of or behind the next, but no more without breaking the line. Conversely, no single trait, structural or physiological, ever evolves by more than a small increment without being accompanied by evolutionary changes in many others. Therefore, no single trait can ever be seen in isolation as a privileged cause of the transition, and so, in principle, there can be no identifiable key innovations (Hunter 1998; Schluter 2000; Galis 2001). To make such a claim would be to ignore the myriad other traits integrated with it. It equally follows that no single trait of an ancestral phenotype can logically be described as a preadaptation. Where a state of preadaptation can be said to exist, it is essentially a property of the phenotype as a whole.
- (ii) The exact sequence in which small changes in different traits occur is more or less random and therefore unpredictable, because there are many different patterns of change that could lead to adaptively modified organisms. Computer simulations of multi-trait evolution, such as those of Niklas (2000) and Lenski *et al.* (2003), lead to the same conclusion, and this point is important for appreciating the nature of adaptive radiations, as well as the evolution of radically new kinds of organisms.
- (iii) No single trait is ever the focus of continuous selection for more than at most a brief period of evolutionary time.
- (iv) Given the very large number of traits that contribute to the overall fitness of the phenotype upon which selection acts, at any given moment many of them cannot be undergoing more than at most very weak selection, and may often evolve by drift. This is in accordance with Haldane's dilemma (Haldane 1957), an issue more familiar in recent years in the context of molecular evolution, and, in principle, also relevant to morphological evolution if evolution simultaneously affects a very large number of traits, as argued here (Williams 1992; Barton & Partridge 2000; Kemp 2007). Selectively neutral, or even slightly deleterious, variants of particular traits can be fixed if they are sufficiently well integrated within what are nevertheless the overall fittest phenotypes.
- (v) The rate of evolution of individual traits will be greatly reduced compared with the rate that is possible under artificial selection, due to a phylogenetic drag imposed on each one by selection for

fitness of the phenotype as a whole. Theoretical models of the evolution of two traits in an adaptive landscape indicate that where the traits are affected differentially by a selective force, they experience a reduced rate of evolution (Wagner 1988). The effect will be even more marked when many traits are considered (Schwenk & Wagner 2001; Merilä & Björklund 2004).

3. APPLYING THE MODEL

The underlying principle of phenotypic integration can scarcely be denied and, while certain details of the correlated progression model developed here may be disputed, the general thrust is surely *realistic*, in so far as it accords with current understanding of the mechanism of evolution. In order to be *useful*, the model must also be capable of generating hypotheses to explain the pattern and sequence of acquisition of traits inferred from the phylogenies of fossil forms related to actual major transitions. That this is indeed the case can be illustrated by a number of examples in which correlated progression has been applied already, and others in which the model clearly has considerable potential explanatory power.

(a) *Mammals*

Recently, Kemp (2006) addressed the long-standing problem of how and why endothermy evolved in mammals. At least five distinct hypotheses existed, each presuming that one or another of the several functions of endothermy in modern mammals was evolutionarily primary and others secondary, and each both supported and contradicted by various pieces of anatomical and physiological evidence. By considering the functional interrelationships between the physiological and structural traits of modern mammals, along with the sequence of acquisition of mammalian traits inferred from the cladogram of the fossil stem group ('non-mammalian' synapsids), he showed how all the many traits associated with endothermy, directly or indirectly, as causes or effects, must have evolved hand in hand. Thus, the novel hypothesis was favoured that the several functions of endothermy actually evolved together, increment by increment, in the pattern predicted by the correlated progression model, rather than any of the hypotheses which assumed that one particular function of endothermy must have been primary.

(b) *Turtles*

A second case in which the correlated progression model has successfully generated a novel hypothesis about a major evolutionary transition is Lee's (1996) study of the origin of the chelonian body plan. By considering the nature of the integration between the parts of modern turtles (figure 2), along with the sequence of acquisition of traits inferred from the phylogeny of the stem group, he was able to hypothesize how the extremely derived chelonian locomotory system, dermal armour and adoption of herbivory could have evolved via a lineage of individually well-integrated phenotypes. His hypothesis stands in contrast to an alternative view of the origin of turtles, expressed most recently by Rieppel (2001), that the rib-vertebrae-carapace-limb complex is too radically

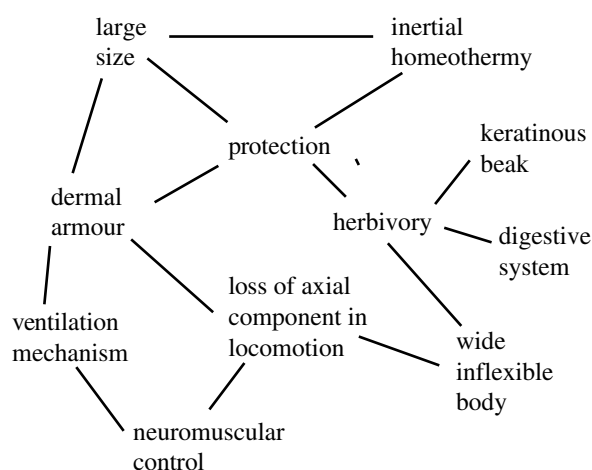


Figure 2. Integration between certain traits of a stem chelonian (redrawn and modified after Lee 1996).

different from the ancestral amniote condition to have evolved gradually, but must have resulted from a macromutational event caused by a radical change in early development. The difficulty with Rieppel's hypothesis is that it must account for how this sudden developmental change also caused what must have been simultaneous, but functionally integrated shifts in many other traits, notably the musculature, limb function, central neural control of locomotion, ventilation mechanism, dietary shift away from faunivory and so on: it is unrealistic in the extreme to suppose that any single macromutation could have such a comprehensive effect. The correlated progression model, in contrast, underpins a hypothesis that is a great deal more in accordance with the current evolutionary and developmental theory, and it also points the way towards an explication of the complex environmental selection pressures responsible for the origin of turtles.

(c) *Invertebrates*

There is rather little evidence, fossil or recent, revealing the sequence of acquisition of the traits of the major invertebrate taxa. Budd (1998) considered the origin of arthropod body plans and, in particular, the paradox of which came first, an internal lever-style musculature or an articulated exoskeleton, when neither could apparently have existed without the other. By explicitly applying the correlated progression model and considering the nature of the functional interrelationship between the two traits, he was able to propose a hypothesis for how they evolved together, increment by increment. He did not extend his analysis to all the other traits that evolved in the course of evolution of the arthropod body plan. Stone & Telford (1999) considered the evolution of rudist bivalves essentially from a correlated progression viewpoint. The nature of the functional interdependence of the several separate traits that underwent changes led them to reject the prevailing hypothesis based on the concept of an identifiable key innovation.

(d) *Tetrapods*

Historically, consideration of the evolutionary process leading to the tetrapods usually consisted of speculating about which single selective force was primarily responsible for driving the transition, variously claimed to be dispersal,

aestivation, avoidance of competition, novel food source, safe breeding sites, etc. (See Olson 1971, pp. 626–634 for a review). Even recently, Carroll *et al.* (2005) have proposed that the adaptive advantage was simply the thermal gain for the animal while temporarily out of the water. The narrowness of such speculation could be attributed, on the one hand, to the absence of adequate information about intermediate grades, and on the other, to an unrealistically simple model of the evolutionary process, in which single traits such as the tetrapod limb or air-breathing are regarded as key innovations.

Recent description of new fossil material of taxa cladistically between ancestral fish-grade tetrapodomorphs, such as *Eusthenopteron*, and definitive early tetrapods, such as *Ichthyostega*, has generated a more extensive cladogram of stem-group tetrapods (figure 3a), necessary for inferring more comprehensively the sequence of acquisition of tetrapod traits (Coates *et al.* 2002; Boisvert 2005; Brazeau & Ahlberg 2006; Daeschler *et al.* 2006; Shubin *et al.* 2006). It is now becoming possible to reconsider the origin of tetrapods explicitly in the light of the correlated progression model.

First, as predicted by the model, there is no evidence that any single trait should be regarded as a key innovation. Rather, the picture that is emerging is one of changes occurring in different parts of the organism in concert. At each node of the cladogram, there are implied evolutionary changes affecting variously the forelimb, pectoral girdle, hind limb, pelvic girdle, axial skeleton, cranial proportions, degree of cranial kinesis, hyomandibular and spiracular notch, and branchial region. Taken together, these traits bear upon the feeding mechanics (a trend away from suction-dominated feeding to grasping-dominated feeding), locomotory mode (a trend away from free-swimming to substrate-based locomotion) and sensory functions (a trend away from strictly water-borne sensory information to increasingly air-borne sound and olfaction). Given these directly inferable changes and what they indicate about increasing use of terrestrial-derived resources, there must also have been correlated evolution of a multiplicity of non-preserved traits associated with increasing physiological tolerance of fluctuating ambient temperature and desiccation, with increasing reliance on a pulmonary and vascular system adapted for aerial ventilation, and with the neural control system.

Second, from a consideration of the nature of the functional interrelationships between all these parts and processes (figure 3b), the correlated progression model leads to a hypothesis about the nature of the selection pressure driving the trend to tetrapods. As so many aspects of the phenotype were evidently affected simultaneously throughout the evolving lineage, a complex multidimensional ecological gradient must have existed, imposing selective demands on a large number of the structures and processes at once. The response of the phenotype, as it slowly traversed the gradient, was integrated incremental changes in feeding, locomotory, sensory, ventilatory, physiological and no doubt life cycle traits.

4. DISCUSSION

For all its relative simplicity and descriptive nature, the correlated progression model of evolution offers a

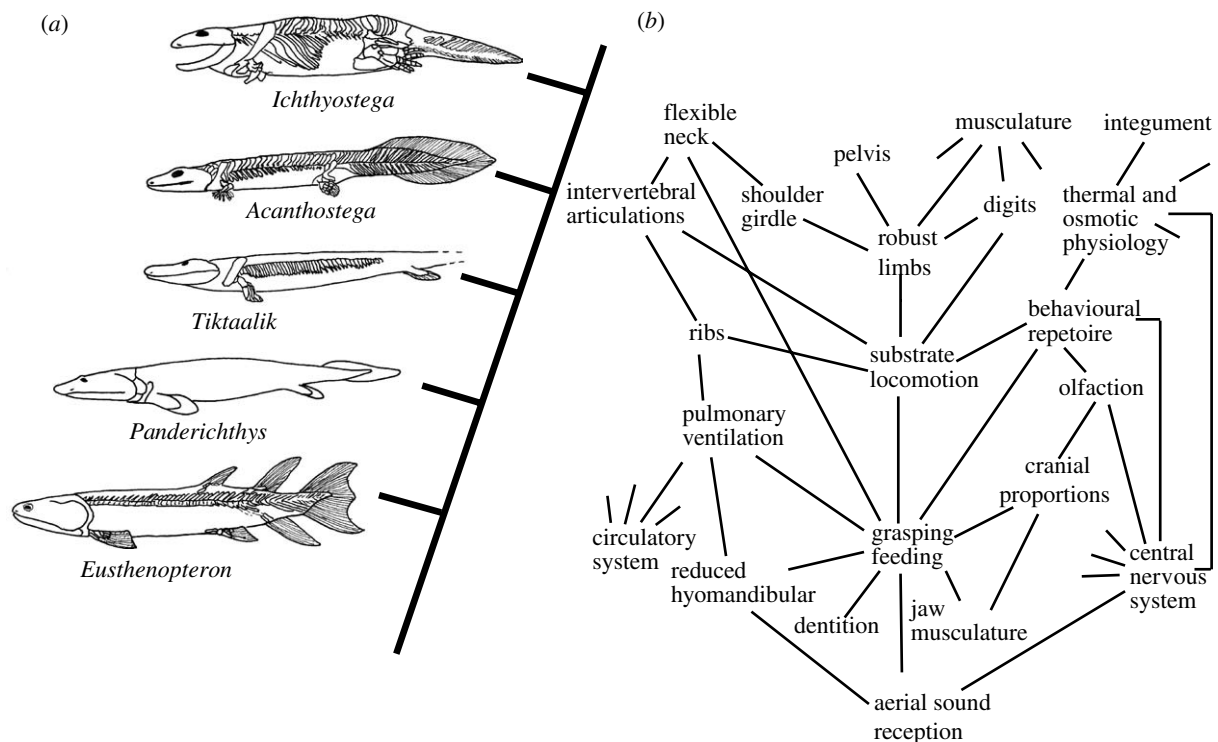


Figure 3. Correlated progression and origin of tetrapods. (a) Cladogram of the better known stem tetrapods (redrawn and modified after Ahlberg & Clack 2006). (b) Postulated pattern of functional linkages between a number of traits of a hypothetical stem tetrapod. The non-connected lines from certain traits represent multiple linkages within the phenotype not individually specified in the diagram.

convincing explanation, in principle, of how integration and evolvability coexist as phenotypic properties across large spans of morphospace. It is congruent with the nature of the interrelationships among the parts and processes of organisms, with the admittedly often rather scant information from the fossil record about the pattern of acquisition of traits in lineages from ancestral to highly derived new taxa, and with the nature of the selective forces believed to act on real organisms in their environments. For these reasons, it may be described as realistic.

It has also been shown to be a usable model for interpreting actual cases of the origin of major new taxa. In the case of mammals, it underpins a specific hypothesis for how and why the multifunctional system of endothermy evolved, despite involving a large number of integrated trait changes, a hypothesis corroborated by the pattern of trait evolution inferred from the fossil record. In the case of turtles, the model is responsible for a hypothesis explaining how the radical redesign of the whole anatomy could evolve without having to invoke a less realistic model based on either developmental revolution or key innovations. For the origin of tetrapods, a case as yet but briefly explored in this light, correlated progression again points to an explanation for how all the evolutionary changes indicated in the fossil record could have evolved without compromising phenotypic integration. Furthermore, the correlated pattern of evolution of traits leads to a hypothesis about the nature of the selective force that acted on the lineage, namely that it was compounded from many ecological dimensions and there must have been a complex ecological gradient from water to land. In all these, and many other cases worthy of investigation from this perspective, increasing fossil evidence

will further corroborate or otherwise the pattern of acquisition of traits predicted by the model.

The correlated progression model effectively rejects an atomistic view of both characters and selective forces, in favour of a systems biology approach to the phenotype and its environment. As a result, it appears somewhat at odds with current systematic and population genetic thinking. Most notable, perhaps, is the implication that the precise sequence of evolutionary changes in the lineage will be below the morphological resolution of the fossil record: if that is indeed the truth of the matter, then it cannot be helped. What the systems mode of thinking does provide are alternative, more pertinent kinds of questions about major evolutionary change. For the phenotype, an appropriate question is: how are the many evolving traits, known and inferred, interrelated functionally in the system as a whole, such that all could evolve increment by increment? For the selective force, an appropriate question is: what was the nature of the multidimensional ecological gradient, affecting the many traits simultaneously, along which the lineage could evolve, incremental shift by incremental shift, to traverse a large tract of morphospace? Both questions are, in principle, answerable from palaeontological information viewed in the light of knowledge of organisms and environments in general.

There are other issues ripe for exploration in the light of the correlated progression model. Most interesting, perhaps, is what roles such mechanisms as pleiotropy, genetic assimilation, heterochrony and shuffling of developmental modules play in the generation of the genetic covariance among many traits that the correlated progression pattern of change represents?

REFERENCES

- Ahlberg, P. E. & Clack, J. A. 2006 A firm step from water to land. *Nature* **440**, 747–749. (doi:10.1038/440747a)
- Alon, U. 2007 *An introduction to systems biology: design principles of biological circuits*. Boca Raton, FL: Chapman and Hall/CRC.
- Barton, N. H. & Partridge, L. 2000 Limits to natural selection. *BioEssays* **22**, 1075–1084. (doi:10.1002/1521-1878(200012)22:12<1075::AID-BIES5>3.0.CO;2-M)
- Boisvert, C. A. 2005 The pelvic fin and girdle of *Panderichthys* and the origin of tetrapod locomotion. *Nature* **438**, 1145–1147. (doi:10.1038/nature04119)
- Brazeau, M. D. & Ahlberg, P. E. 2006 Tetrapod-like middle ear architecture in a Devonian fish. *Nature* **439**, 318–321. (doi:10.1038/nature04196)
- Budd, G. E. 1998 Arthropod body-plan evolution in the Cambrian with an example from anomalocaridid muscle. *Lethaia* **31**, 197–210.
- Budd, G. E. 2006 On the origin and evolution of major morphological characters. *Biol. Rev.* **81**, 609–628. (doi:10.1017/S1464793106007135)
- Carroll, R. L., Irwin, J. & Green, D. M. 2005 Thermal physiology and the origin of terrestriality in vertebrates. *Zool. J. Linn. Soc.* **143**, 345–358. (doi:10.1111/j.1096-3642.2005.00151.x)
- Ceste, M. E. & Doyle, J. C. 2002 Reverse engineering of biological complexity. *Science* **295**, 1664–1669. (doi:10.1126/science.1069981)
- Coates, M. I., Jeffery, J. E. & Ruta, M. 2002 Fins to limbs: what the fossils say. *Evol. Dev.* **4**, 390–401. (doi:10.1046/j.1525-142X.2002.02026.x)
- Daeschler, E. B., Shubin, N. H. & Jenkins Jr, F. A. 2006 A Devonian tetrapod-like fish and the evolution of the tetrapod body plan. *Nature* **440**, 757–763. (doi:10.1038/nature04639)
- Dassow, G. v. & Munro, E. 1999 Modularity in animal development and evolution: elements of a conceptual framework for evodevo. *J. Exp. Zool. (Mol. Dev. Evol.)* **285**, 307–325. (doi:10.1002/(SICI)1097-010X(19991215)285:4<307::AID-JEZ2>3.0.CO;2-V)
- Dullemeijer, P. 1974 *Concepts and approaches in animal morphology*. Assen, The Netherlands: Van Gorcum.
- Eble, G. J. 2004a The macroevolution of phenotypic integration. In *Phenotypic integration: studying the ecology and evolution of complex phenotypes* (eds M. Pigliucci & K. Preston), pp. 253–273. Oxford, UK: Oxford University Press.
- Eble, G. J. 2004b Morphological modularity and macroevolution: conceptual and empirical aspects. In *Modularity: understanding the development and evolution of natural complex systems* (eds W. Callebaut & D. Rasskin-Guttmann), pp. 221–238. Cambridge, MA: MIT Press.
- Galis, F. 2001 Key innovations and radiations. In *The character concept in evolutionary biology* (ed. G. P. Wagner), pp. 583–607. San Diego, CA: Academic Press.
- Griswald, C. K. 2006 Pleiotropic mutation, modularity and evolvability. *Evol. Dev.* **8**, 81–93. (doi:10.1111/j.1525-142X.2006.05077.x)
- Haldane, J. B. S. 1957 The cost of natural selection. *J. Genet.* **55**, 511–524.
- Hunter, J. P. 1998 Key innovations and the ecology of macroevolution. *Trends Ecol. Evol.* **13**, 31–36. (doi:10.1016/S0169-5347(97)01273-1)
- Kemp, T. S. 1985 Synapsid reptiles and the origin of higher taxa. *Spec. Pap. Palaeontol.* **33**, 175–184.
- Kemp, T. S. 1999 *Fossils and evolution*. Oxford, UK: Oxford University Press.
- Kemp, T. S. 2006 The origin of mammalian endothermy: a paradigm for the evolution of complex biological structure. *Zool. J. Linn. Soc.* **147**, 473–488. (doi:10.1111/j.1096-3642.2006.00226.x)
- Kemp, T. S. 2007 The origin of higher taxa: macroevolutionary processes, and the case of the mammals. *Acta Zool.* **88**, 3–22. (doi:10.1111/j.1463-6395.2007.00248.x)
- Kirschner, M. & Gerhart, J. 1998 Evolvability. *Proc. Natl Acad. Sci. USA* **95**, 8420–8427. (doi:10.1073/pnas.95.15.8420)
- Konopka, A. K. 2007 Basic concepts of systems biology. In *Systems biology: principles, methods, and concepts* (ed. A. K. Konopka), pp. 1–26. Boca Raton, FL: Taylor and Francis/CRC.
- Lee, M. S. Y. 1996 Correlated progression and the origin of turtles. *Nature* **379**, 812–815. (doi:10.1038/379812a0)
- Lenski, R. E., Ofria, C., Pennock, R. T. & Adami, C. 2003 The evolutionary origin of complex features. *Nature* **423**, 139–144. (doi:10.1038/nature01568)
- Lewontin, R. C. 1974 *The genetic basis of evolutionary change*. New York, NY: Columbia University Press.
- Merilä, J. & Björklund, M. 2004 Phenotypic integration as a constraint and adaptation. In *Phenotypic integration: studying the ecology and evolution of complex phenotypes* (eds M. Pigliucci & K. Preston), pp. 107–129. Oxford, UK: Oxford University Press.
- Nagy, L. M. & Williams, T. A. 2001 Comparative limb development as a tool for understanding the evolutionary diversification of limbs in arthropods: challenging the modularity paradigm. In *The character concept in evolutionary biology* (ed. G. P. Wagner), pp. 457–490. San Diego, CA: Academic Press.
- Niklas, K. J. 2000 Modelling fossil plant form–function relationships: a critique. In *Deep time: paleobiology's perspective* (eds D. H. Erwin & S. L. Wing), pp. 289–304. Washington, DC: The Paleontological Society.
- Olson, E. C. 1971 *Vertebrate paleozoology*. New York, NY: Wiley.
- Palsson, B. O. 2006 *Systems biology: properties of reconstructed networks*. Cambridge, UK: Cambridge University Press.
- Rieppel, O. 2001 Turtles as hopeful monsters. *BioEssays* **23**, 987–991. (doi:10.1002/bies.1143)
- Schlosser, G. 2002 Modularity and the units of selection. *Theor. Biosci.* **121**, 1–80. (doi:10.1078/1431-7613-00049)
- Schlosser, G. 2004 The role of modules in development and evolution. In *Modularity in development and evolution* (eds G. Schlosser & G. P. Wagner), pp. 519–582. Chicago, IL: University of Chicago Press.
- Schluter, D. 2000 *The ecology of adaptive radiation*. Oxford series in ecology and evolution. Oxford, UK: Oxford University Press.
- Schwenk, K. & Wagner, G. P. 2001 Function and evolution of phenotypic stability: connecting pattern and process. *Am. Zool.* **41**, 552–563. (doi:10.1668/0003-1569(2001)041[0552:FATEOP]2.0.CO;2)
- Schwenk, K. 2001 Functional units and their evolution. In *The character concept in evolutionary biology* (ed. G. P. Wagner), pp. 167–200. San Diego, CA: Academic Press.
- Shubin, N. H., Daeschler, E. B. & Jenkins Jr, F. A. 2006 The pectoral fin of *Tiktaalik roseae* and the origin of the tetrapod limb. *Nature* **440**, 764–771. (doi:10.1038/nature04637)
- Stone, J. R. & Telford, M. 1999 Using critical path method to analyse the radiation of rudist bivalves. *Palaeontology* **42**, 231–242. (doi:10.1111/1475-4983.00072)
- Thomson, K. S. 1966 The evolution of the tetrapod middle ear in the rhinidistian–amphibian transition. *Am. Zool.* **6**, 379–397.

- Wagner, G. P. 1988 The influence of variation and of developmental constraints on the rate of multivariate phenotypic evolution. *J. Evol. Biol.* **1**, 45–66. (doi:10.1046/j.1420-9101.1988.1010045.x)
- Wagner, G. P. 2001 *The character concept in evolutionary biology*. San Diego, CA: Academic Press.
- Wagner, G. P. & Altenberg, L. 1996 Complex adaptations and the evolution of evolvability. *Evolution* **50**, 967–976. (doi:10.2307/2410639)
- Wagner, G. P. & Laubichler, M. D. 2000 Character identification in evolutionary biology: the role of the organism. *Theor. Biosci.* **119**, 20–40. (doi:10.1078/1431-7613-00003)
- West-Eberhard, M. J. 2003 *Developmental plasticity and evolution*. Oxford, UK: Oxford University Press.
- Williams, C. G. 1992 *Natural selection: domains, levels, and challenges*. *Oxford series in ecology and evolution*. Oxford, UK: Oxford University Press.